

CHAPTER THIRTY

EVOLUTIONARY PROCESSES IN THE TASMANIAN HIGH ALTITUDE EUCALYPTS

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INTRODUCTION

The rugged Tasmanian topography results in a patchy distribution of treeline habitat, which can be viewed as a mosaic of "habitat islands" varying considerably in size and degree of isolation. In recent geological time the Pleistocene glacial cycles have subjected this mosaic to dramatic perturbation involving habitat relocation, fragmentation, coalescence and, on a local scale, extinction and birth of unique adaptive modes. In this paper we examine the adaptive response of populations to a fluctuating mosaic of selective forces through a discussion of the evolution of clines in the Tasmanian high altitude eucalypts.

The eucalypts primarily associated with the treeline habitat in Tasmania (i.e. E. coccifera*, E. urnigera, E. vernicosa and E. gunnii) are all endemic. Populations of these species are distributed as mosaics or disjunctions within more continuous and widespread populations of subalpine and lowland taxa (e.g. E. delegatensis, E. dalrympleana, E. pauciflora, E. nitida). In many cases, there is a geographic and genetic continuum between stunted treeline variants and surrounding subalpine forest variants resulting in complex genetic mosaics. The range of variation along these altitudinal gradients is often large, transgressing several recognized taxa. The origin of these multi-character, clinal mosaics is of particular theoretical interest. These may arise as a result of either primary or secondary intergradation and it is important from an evolutionary viewpoint to differentiate these alternatives, although this is difficult from population structure alone (Anderson 1953; Barber and Jackson 1957; Mayr 1963; Endler 1977; Potts and Reid 1985b).

Specific hypotheses accounting for the origin of clinal mosaics include:

1. Primary intergradation (parapatric differentiation)
 - (a) parallel evolution
 - (b) fragmentation of once geographically extensive clines

* nomenclature follows Pryor and Johnson (1971)

2. Secondary intergradation

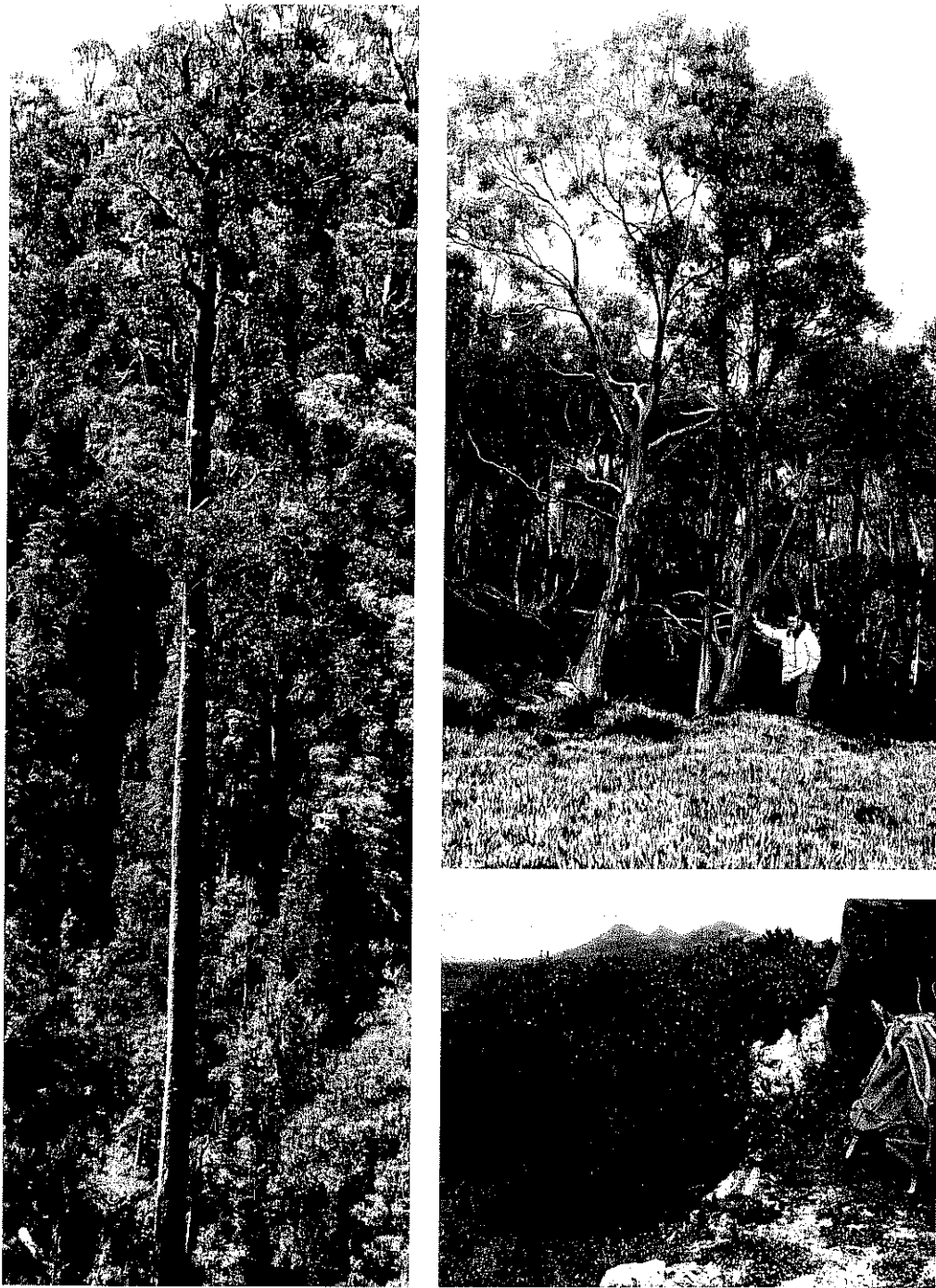
- (a) range fragmentation and introgression associated with a break down in
 - (i) geographic isolation
 - (ii) local reproductive isolation
- (b) long distance migration by
 - (i) seed dispersal
 - (ii) pollen dispersal

Possible examples of virtually all these alternatives can be found in the Tasmanian eucalypts, and the intricate variation patterns in specific complexes probably integrate the full spectrum of these evolutionary processes.

PRIMARY DIFFERENTIATION

Several possible examples of parapatric differentiation in the Tasmanian high altitude eucalypts have been reported (Barber and Jackson 1957; Jackson 1960; Potts and Reid 1985a,b). The most dramatic must be the clines in *E. vernicosa* detailed by Jackson (1960), from the tall subalpine forest form classified as subsp. "johnstonii" (i.e. cline-forms "johnstonii" and "columnaris" *sensu* Jackson 1960, Fig. 1), through subsp. "subcrenulata" (Fig. 2), to the alpine shrub subsp. "vernica" (Plate 3). The subsp. vernica variant is confined to alpine shrubberies on the pre-Carboniferous mountains of western Tasmania and is a unique eucalypt in being a shrub and frequently reproductively mature when less than 0.35 m high. The continuum in *E. vernica* involves clinal variation in numerous morphological, anatomical, and growth characters which vary as a response to increasing exposure to the alpine environment (Fig. 4). The full spectrum of forms can be found in the continuous stands on Mt Arrowsmith, for example, where there is a smooth altitudinal transition in morphology from the tall forest variants, emergent above a dense rainforest at the base, to the subsp. vernica form in the shrubbery near the summit (Fig. 5).

The full spectrum of variants is rarely found on a single mountain block due to either a limited altitudinal range or exclusion from part of the selective gradient by other vegetation (e.g. rainforest - Jackson 1968; Kirkpatrick and Harwood 1980). Nevertheless, varying sections of the continuum are repeated, with neighbouring mountains frequently demonstrating parts of the cline absent on a given mountain. Morphological discontinuities only arise when the population is discontinuously distributed along the environmental gradient. In addition, the exposure gradient which is usually associated with increasing altitude may be markedly displaced by geographical position, aspect and soil fertility. For example, increased exposure on the southern and western flanks of mountains causes a downward displacement of the cline, with the lower end being displaced by about 250 metres between northeastern and southwestern aspects. The cline is intensified by local areas of infertility and waterlogging, where the absence of protective dominants greatly increases exposure. In contrast, the stepped topography in eastern Tasmania associated with plateaux development results in



Figs. 1-3. *Eucalyptus vernicosa*. 1. Tall forest tree variant (subsp. "columnaris", see Fig. 1), in a mixed forest at the base of Mt Arrowsmith. 2. The intermediate cline-form (subsp. "subcrenulata", right) with *E. coccifera* (left) in a subalpine woodland. 3. The alpine shrub variant (subsp. vernica) near the summit of Mt Arrowsmith

extensive populations being stabilized at a similar adaptive level. This is also seen in *E. gunnii* where clines associated with increasing exposure to the alpine environment on the Central Plateau directly reflect the underlying topography (Fig. 6), with local steepening of the clines being associated with steps between erosion surfaces. In the case of *E. gunnii*, the widely distributed open woodland form around Great Lake was given specific status (*E. divaricata*, Brett 1938), although when viewed in the context of the full range of variation within *E. gunnii* (Potts and Reid

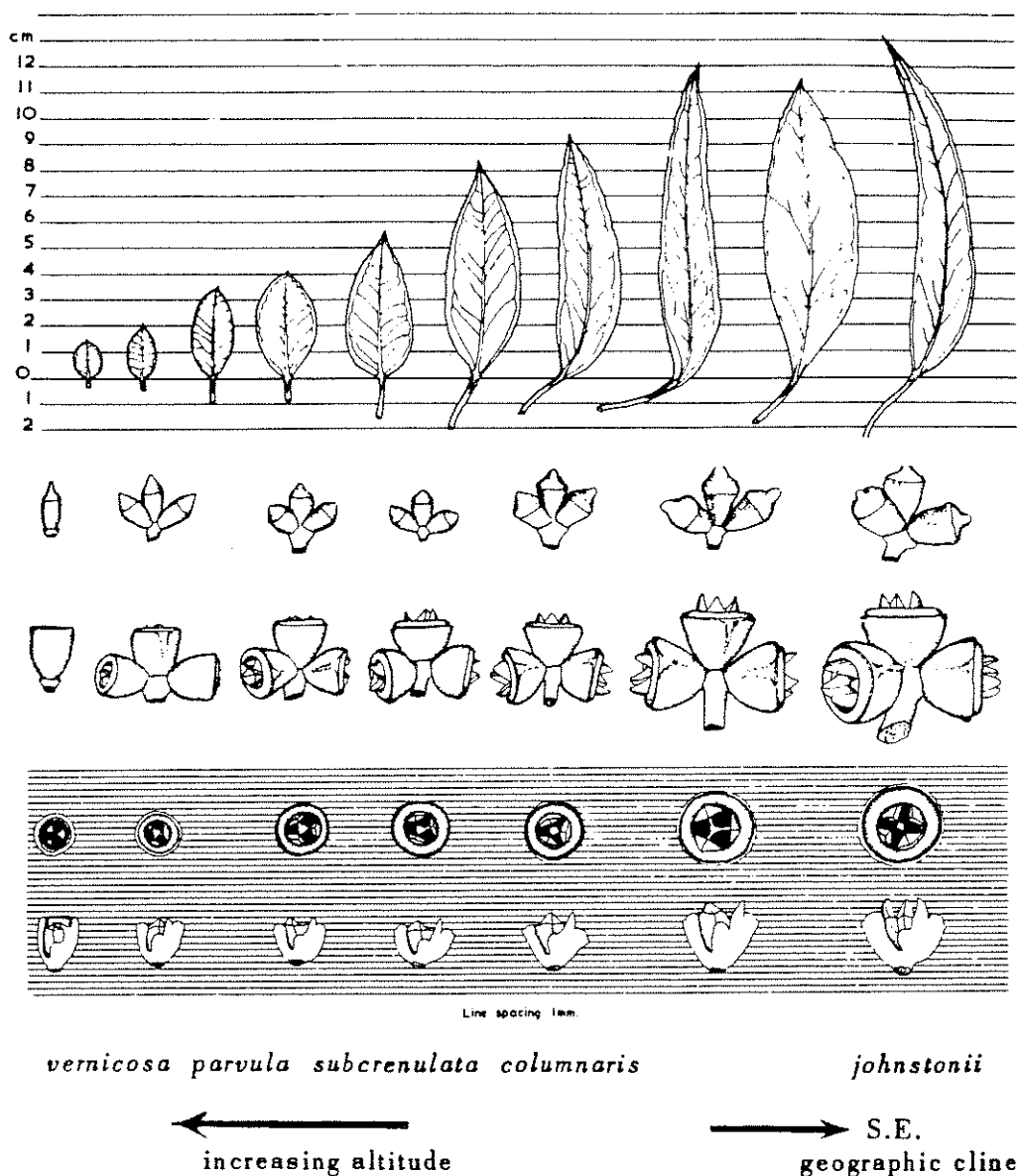


Fig. 4. Typical leaves, buds and fruits of the cline forms of *E. vernicosa* showing the gradient in characters altitudinally (from centre towards left) and with geographical displacement (from centre towards right) (from Jackson 1960)

1985a,b) these populations clearly represent an extensive patch of an intermediate cline-form. However there is also evidence for partial barriers to gene flow along this exposure cline and the "*divaricata*" stands around Great Lake flower over 1.5 months earlier than contiguous stands at higher and lower altitudes (Fig. 6).

Stepped clines have also been described in *E. urnigera* (Barber and Jackson 1958; Barber 1965; Thomas and Barber 1974a,b), a species closely related to *E. gunnii*. Over a smooth altitudinal change of about 200 m (less than 1 km ground distance) on Mt Wellington, there is a complete transition in the frequency of glaucous phenotypes (Fig. 7). Phenotypes in a closed, wet sclerophyll forest at the lower altitudinal range (560-670 m) are uniformly green while those near the treeline (900-1050 m) are

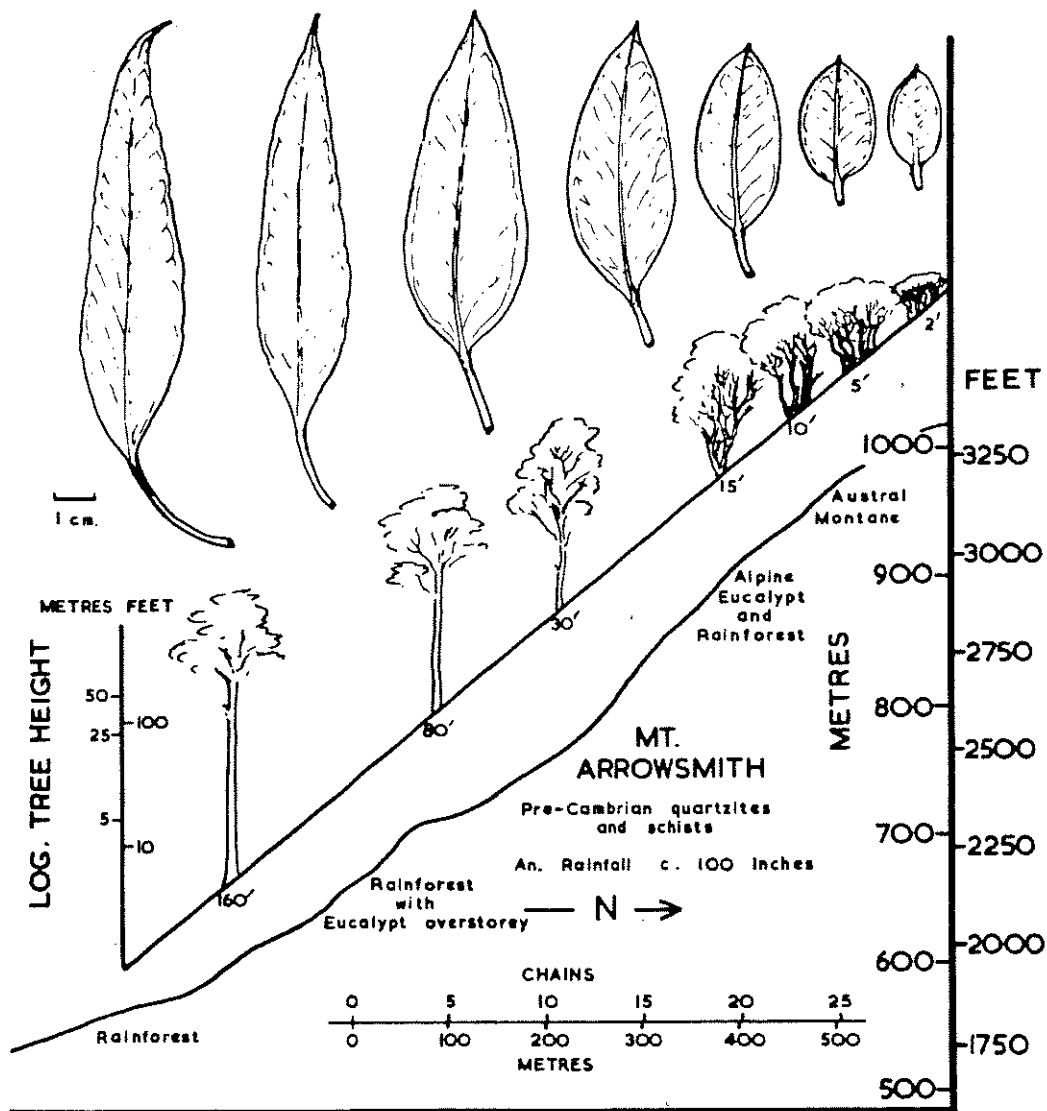


Fig. 5. Clinal variation in height, habit and leaf morphology in the continuous stands of *E. vernicosa* on the southern slope of Mt Arrowsmith in western Tasmania (from Jackson 1960)

uniformly glaucous. It is possible that the steepening of the cline in glaucousness is a response to a step in a primary selective gradient which is not linearly related to altitude. More likely, however, this steep cline results from convergence toward an equilibrium position along an environment gradient. Endler (1977, p. 164), using estimates of the cline parameters, has shown that the observed cline is better fitted to a gradient than an ecotone model. Extreme morphs along this cline are

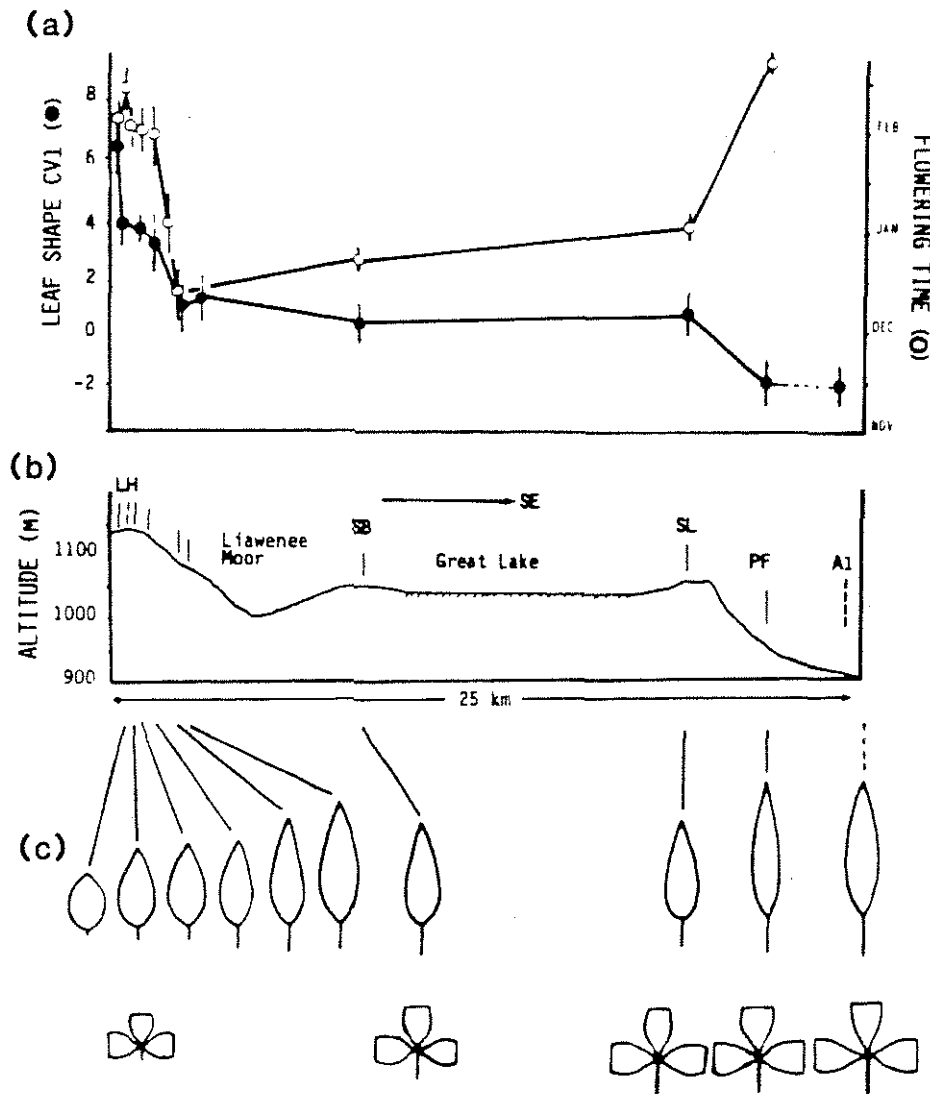


Fig. 6. Clinal variation in *E. gunnii* along an altitudinal transect on the Central Plateau, Tasmania. (a), Population means and 95% confidence limits for the first canonical variate derived from analysis of adult leaf dimensions (solid circles) and the mean (\pm SE) flowering time in the 1980 season (open circles). (b), Topographic cross section. (c), Leaf and inflorescence ideograms based on character means (from Potts and Reid 1985a)

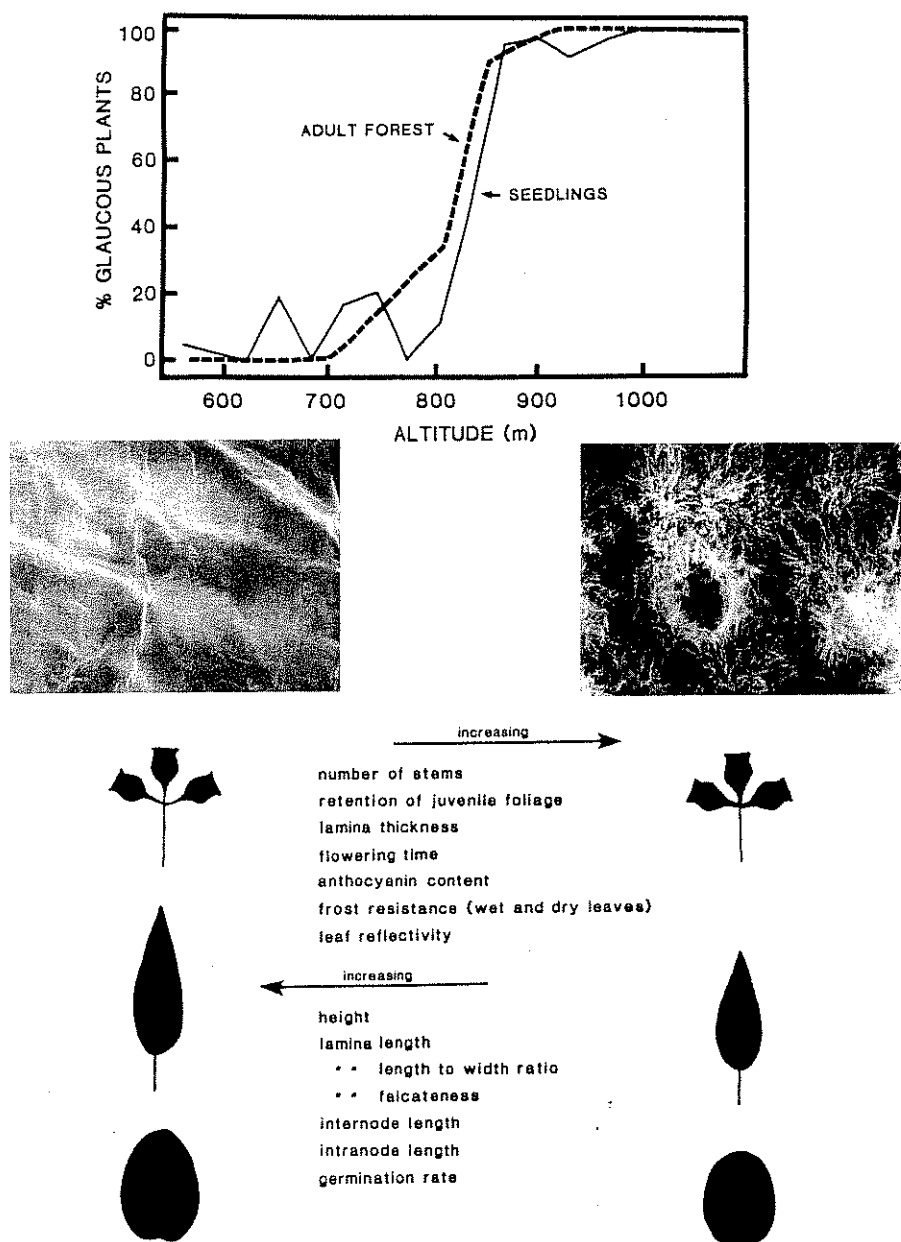


Fig. 7. Clinal variation in glaucousness in *E. urnigera* on Mt Wellington, Tasmania (modified from Barber and Jackson 1957). Electron micrographs of the adaxial surface of young seedling leaves from green (left) and glaucous (right) variants and ideograms of inflorescences and adult (X 0.34) and seedling leaves. Ideograms are based on character means from population samples from the lower and upper altitudinal limits. Characters exhibiting significant differences between green and glaucous phenotypes are listed and their direction of increase is indicated (data compiled from Barber and Jackson 1957; Barber 1965; Thomas and Barber 1974a,b, and unpub. data)

differentiated in numerous characters other than glaucousness (Fig. 7) and, while their exact pattern of response is not fully known, Barber (1965) noted that such correlated clines may result from either pleiotropic gene action or separate acts of selection. While the latter is assumed for the cline in *E. urnigera* (Barber 1965), in *E. gunnii* parallel multi-character clines appear to involve characters which are pleiotropically or developmentally inter-related as well as characters which are "selectively linked" (Potts and Reid 1985b).

EVOLUTION OF REPRODUCTIVE ISOLATION

Barber (1965) suggested that correlated selection will tend to steepen independent clines, particularly around a discontinuity or step in habitat or around local steps in a genetic cline of high adaptive value (e.g. glaucousness). He inferred that concordant steep clines are but a step away from parapatric speciation. It is argued that as concordant clines steepen, an increasing number of individuals or gametes, differing in an increasing number of selectively correlated alleles, will disperse into an unfavourable environment, thus increasing the selective pressure for a reduction in gene flow. However Crosby (1970) argued that selection to reduce the disruptive effect of gene flow is a second-order event and is likely to be less effective than the direct selection processes normally encountered. This will be the case particularly where density-dependent selection is important (Barber 1965). While equilibrium models suggest that parapatric speciation is possible (e.g. Caisse and Antonovics 1978), the latter phase of this process is probably highly sensitive to fluctuations in the underlying selective regime and, in long-lived temperate forest-tree species such as eucalypts, it is unlikely that there has been sufficient environmental stability in recent geological times to allow completion of the process envisaged by Barber (1965). This problem would be accentuated along gradients, as opposed to ecotones, where slight fluctuations in the underlying selective regime may cause large geographic shifts in the null points of clines (see Potts 1985b).

A more rapid, and possibly more common, mechanism has been detailed by Potts and Reid (1985a), and would explain the partial barriers to gene flow which would arise from the steep clines in flowering time which parallel the phenetic clines in *E. gunnii* (Fig. 6). The clines in flowering time are suggested to result from direct adaptation of the reproductive system to the same ecological gradient, with a reduction in gene flow being incidental. Regardless of whether the initial partial barrier is genetic or plastic, it may be significant in increasing the rate of differentiation and establishing concordance of independent clines (e.g. Endler 1977). Where strong gradients initiate simultaneous clinal variation in many characters, reduced gene flow is probably common, enhancing the rate of divergence and forming a foundation for the evolution of more stable isolating mechanisms.

THE ROLE OF SELECTION

While there is no unambiguous evidence to fully dismiss the hypothesis of secondary intergradation, there is little doubt that the clines

detailed are adaptive, and that disruptive selection is a prime factor maintaining differentiation. For the E. vernicosa clines, this is evidenced by the close association of the phenetic variants with variation in ecological factors (i.e. exposure to the alpine environment), an association which is repeated within numerous isolated populations and maintained over 240 km of latitude and 80 km of longitude. There is no indication of increased variability in intermediate regions of the cline which might be expected during the early stages of secondary intergradation. However there is a trend for populations at higher altitudes to be the more variable, explained by greater variation in micro-climate at high altitudes (Jackson 1960). In E. urnigera, selection coefficients have been calculated by assuming the cline is in equilibrium and comparing the frequency of glaucous phenotypes in adults and an unselected seedling cohort. These estimates (Barber and Jackson 1957; Endler 1977) indicate intense spatial variation in selection coefficients. This variation maintains the cline between green and glaucous phenotypes despite a 5-10% reproductive loss through reciprocal immigration or segregation of unfit gametes. Moreover, later physiological work (Thomas and Barber 1974a,b) has suggested the specific adaptive significance of variation in glaucousness. Experimental gardens established along the altitudinal gradient in E. gunnii have similarly indicated a selective differential between extreme morphs. Seedlings from the treeline population are unable to compete with the faster growing, low altitude variants at the latter site, whereas at the treeline, there was greater mortality of seedlings from the low altitude populations than those from the treeline population (Potts 1985a). However, while these trials suggest that differentiation within these more or less continuous stands is at least partly maintained by disruptive selection, there is no direct evidence as to whether the phenetic clines are adaptive per se or merely associated with other, perhaps physiological, characters more closely related to fitness.

A secondary argument for the adaptive significance of many of these genetically based clines is obtained from parallelisms in the variation patterns in a taxonomically diverse range of species (Barber 1955; Potts and Reid 1985a). A common genetic response of most species to exposure to the alpine environment involves a reduction in growth rate coupled with a decrease in leaf size and an increase in lamina thickness (Pryor 1957; Jackson 1960; Potts and Reid 1985b). In addition, the retention of the "juvenile" or "intermediate" foliage type into the reproductively mature phase occurs at the upper altitudinal limit in E. coccifera, E. gunnii, E. urnigera and E. vernicosa and is indicative of a general trend for these foliage types to be retained longer in extreme environments of exposure and drought (Potts and Reid 1985b). Neotenic and paedomorphic processes may allow rapid and extensive differentiation of the adult phenotype with the minimum of genetic restructuring and these processes have probably been a significant factor in eucalypt evolution (Barber 1965; Potts and Reid 1985b).

SECONDARY INTERGRADATION

Climatic change during the Pleistocene would have resulted in a complex pattern of barrier formation and removal associated with both warming and cooling phases of the glacial cycles. Kirkpatrick and Brown (1984) envisaged range oscillations in high altitude species, with small populations stranded on high ground during inter-glacials, expanding and coalescing during glacial periods. Populations would have also been isolated by low glacial treelines and there is some evidence for a major glacial barrier between northern and southern high altitude eucalypt floras which would have acted as a barrier to invasion of mainland species and radiation from a southeastern glacial refugium (see Davies 1974; Kirkpatrick and Brown 1984; Potts and Reid 1985b; Kirkpatrick 1986). This is supported by the absence of *E. coccifera*, *E. urnigera* and the *E. vernicosa* cline forms from what appear to be suitable habitats on the northeastern mountains.

Several clines in the Tasmanian high altitude eucalypts have been attributed to secondary contact following population migration after the Last Glacial (Shaw *et al.* 1984; Potts and Reid 1985b). The continuum between green (subsp. *archeri*) and glaucous (subsp. *gunnii*) subspecies of *E. gunnii* on the Western Tiers in Central Tasmania, for example, is thought to represent a stabilized zone of secondary intergradation between populations isolated in the north (subsp. *archeri*) and south (subsp. *gunnii* - "*divaricata*" variant) (Potts and Reid 1985a,b; Fig. 8). The Western Tiers probably represent a local suture-zone (Remington 1968), and due to glaciation, intermediate populations on top clearly occur in the younger, and possibly most disturbed, habitat. Extreme morphs have probably differentiated in a clinal manner through a series of possibly allopatric populations. These extreme morphs probably contacted as suggested for "ring species" (Endler 1977), although in this case prior to the development of reproductive barriers of sufficient strength to prevent extensive introgression.

Detailed analysis of the structure of this zone of intergradation (Potts and Reid 1985a,b) indicates that it involves parallel clines in numerous characters, and compounds altitudinal variation with a north-south geographic cline between subspecies (cf. Fig. 8). The genetic stability and widespread distribution of intermediate phenotypes, the general absence of strong character associations, and the failure of peaks of variability to coincide all suggest that the continuum is not of recent origin. In fact, estimates of the postglacial climatic regime (e.g. Macphail 1979) suggest that if secondary contact occurred as hypothesized, this was probably about 30-40 generations ago, which would allow many generations for selective stabilization. Neutral secondary contact can be excluded (Barber 1955; Potts 1985a). However, the intensity of selection may vary markedly between characters which may explain the general increase in variability in reproductive, as opposed to vegetative characters, observed in several intermediate populations (Potts and Reid 1985a).

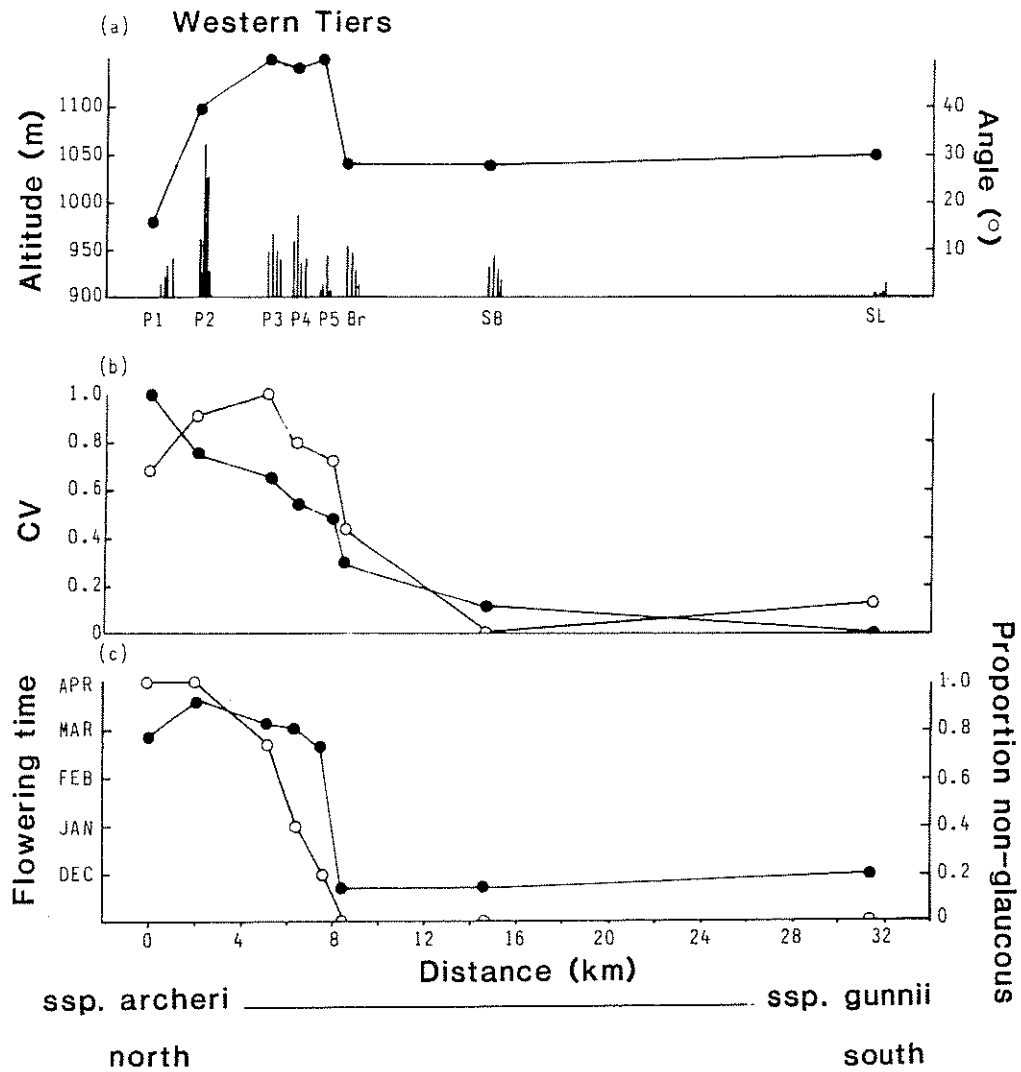


Fig. 8. Environmental and phenetic variation in *E. gunnii* over the Western Tiers, Tasmania (from Potts and Reid 1985a). **(a)**, Variation in altitude (dots) and horizon cut-off angles (columns) taken from NW, W, SW and S bearings. **(b)**, Variation in CV1 (open circles) and CV2 (solid circles) derived from canonical variates analysis of 15 adult morphometric characters and based on population samples from throughout the geographic range of *E. gunnii*. CV1 was highly correlated with altitude, whereas CV2 mainly differentiated subsp. *archeri* from subsp. *gunnii*. Canonical variates have been standardized to unit range. **(c)**, Variation in the proportion of non-glaucous individuals (open circles) and the mean flowering time in the 1980 season (solid circles)

POPULATION MIGRATION

The dynamics of migration must be examined to fully understand the response of populations to a fluctuating selective mosaic. In the lowland flora, the dynamics of population migration associated with a selective disequilibrium at the boundary between two closely related species have been examined (Potts 1985b). There is a marked inertia in population response due to extremely slow population turnover and limited dispersal potential (cf. Davis 1981). Furthermore, fluctuations in the selective regime at a boundary may result in the breakdown of delicate barriers to hybridization between closely related species, which in eucalypts have both a genetic and ecological basis (Pryor 1976). Where seed migration is limited, boundary movements may be heralded by a wave of hybridization due partly to pollen swamping of the species with the lowest fitness (Potts 1985b). Hybrid swarms may develop but, at the boundary of large stands at least, are probably transitory.

Invasion of habitat islands

While species replacement will often occur along continuous migration routes (e.g. altitudinal shifts), the patchy nature of the environment will frequently prevent or retard migration as a front. Adaptation to habitat islands within a species range (created by climatic change for example) may then occur by in situ parapatric or sympatric differentiation from variation inherent within the local gene-pool or by long distance migration of a pre-adapted species (or genotype). In the absence of competition, viable populations can probably be maintained on such ecologically marginal sites, particularly when supplemented by dispersal from surrounding sites. However, an evolutionary response will depend on the relative probability of local adaptation versus long distance invasion, and this will depend on numerous factors (e.g. genetic diversity, degree of isolation, dispersal potential, patch size, etc.; cf. MacArthur and Wilson 1967).

The modes of invasion of habitat islands within the range of a potentially interbreeding species are shown in Fig. 9. The mechanism of invasion by pollen migration has been detailed in several low altitude eucalypts (Potts and Reid 1983; Potts 1983) and may be an effective mechanism of species migration in taxa where reproductive barriers are weak and seed migration is limited. This mechanism involves long distance pollen dispersal and hybridization followed by back-selection to the co-adapted gene combinations of the pollen parent from a segregating hybrid swarm. Character cohesion will tend to increase the probability of parental gene combinations being derived by segregation (e.g. Hartley 1965), as will subsequent backcrossing resulting from other dispersal events. Alternatively, if the habitat is suited to a combination of parental characteristics, selection may result in the stabilization of a hybrid product. Even where the initial founder event occurs by long distance seed migration, the proximity of the founder to plants of the other species and pollen swamping from the more common species (see Lewis 1961; Levin 1978a,b; 1983) may result in a phase of hybridization in an expanding founder population which would allow ample opportunity for adaptive or non-adaptive gene exchange. At one extreme of hybrid fitness, this may result in an "invasion cline" (see Baker 1951); at the other extreme, the selective pressure for the displacement of reproductive

characters to avoid hybridization (i.e. Wallace Effect; Grant 1971) will be maximized in small founder populations.

Population extinction

The upslope migration of populations on many isolated mountains and hills following deglaciation would have seen a contraction of population size, in many cases culminating in extinction. There are many small populations of these high altitude eucalypts isolated at relatively low altitudes on peripheral hills and mountains throughout Tasmania (particularly the southeast) and there is little doubt that they represent

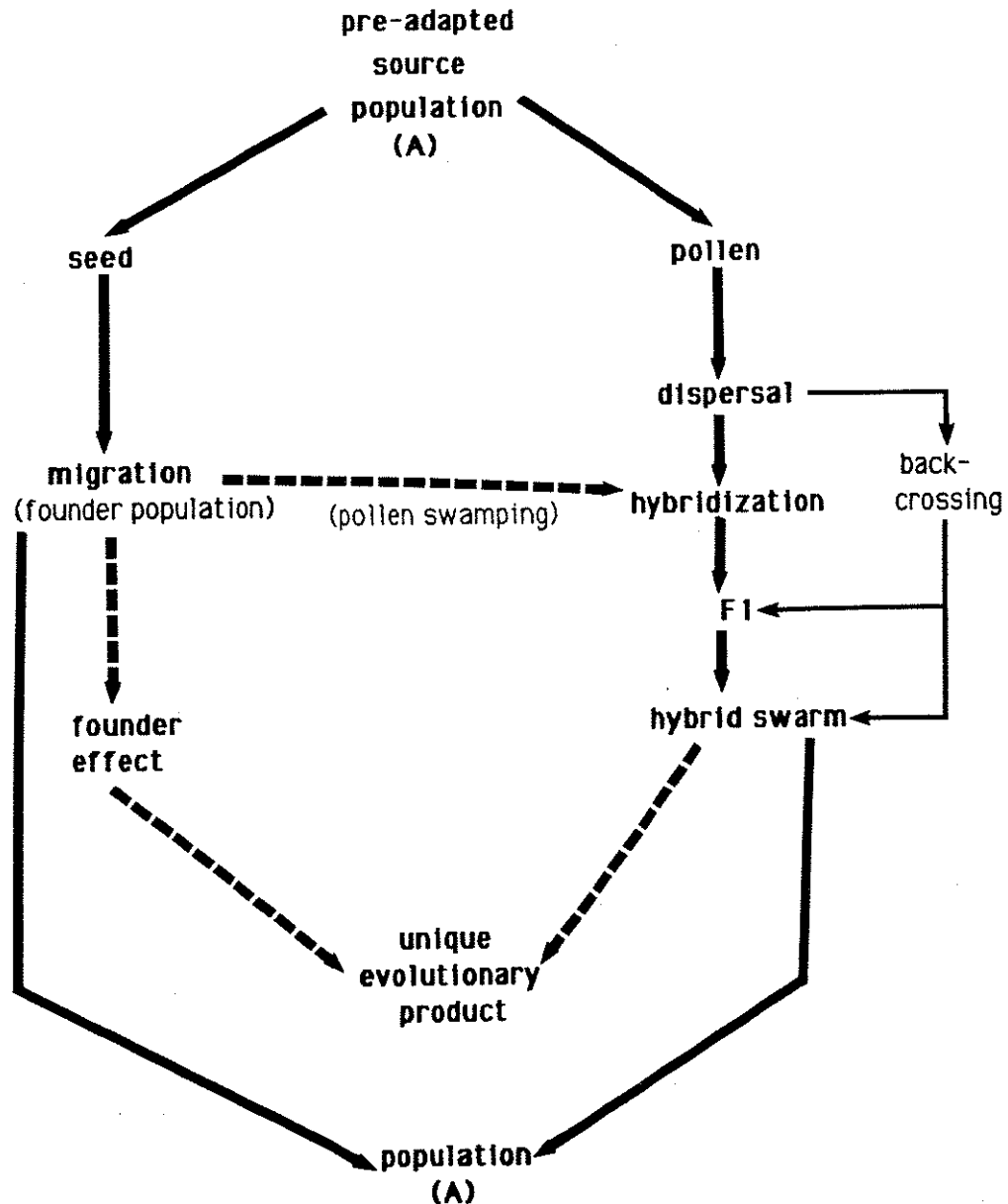


Fig. 9. Modes of invasion of habitat islands within the range of a potentially interbreeding species

the remnants of a more continuous glacial distribution. In E. gunnii, many of the small peripheral isolates in the east are phenetically unique and highly variable (Potts and Reid 1985a), and in many cases this appears to be the result of hybridization with surrounding lowland species (Potts and Reid 1985b). While hybridization may not seem important at the boundary of large stands, it may have important evolutionary consequences in small peripheral isolates where the nucleus of the stand may contract to the point where selection is unable to counter-balance pollen swamping from surrounding more abundant species (see Kirkpatrick et al. 1973; Potts and Reid 1985b). Genetic invasion may eventually result in phantom hybrid populations (e.g. Parsons and Kirkpatrick 1972) and even the assimilation of the genetic remnants into the gene-pool of the invading species (e.g. Baker 1951; Harland and de Wet 1963). In contrast, slow gene exchange with contiguous species may be one means by which small relict populations may retain evolutionary flexibility (Kirkpatrick 1976).

In some cases, specific integrity may only be broken down in the last stages of extinction when pollen swamping is at a maximum, resulting in localized introgressed patches. Several peripheral isolates of E. gunnii appear to demonstrate this process. However, when reproductive barriers are poorly established introgression may be more widespread and this seems to be the case for E. coccifera and E. nitida detailed by Shaw et al. (1984). For most of their geographic range these species occur in entirely different regions of the island. However, on transitional mountains both co-occur and extensive populations of E. nitida at the base clinally intergrade into forms resembling E. coccifera at higher altitudes. On mountains such as Tim Shea, intermediates extend over a considerable altitudinal range and only small patches of the more extreme phenotypes resembling E. coccifera occur near the summit. It is argued that these patches and associated clines are probably a result of the upslope migration and radiation of E. coccifera into the range of E. nitida since the Last Glacial (Shaw et al. 1984). The small patch near the summit of Tim Shea, for example, appears to have been swamped by E. nitida genes to the point where it is approaching a phantom hybrid population and the altitudinal clines probably partly reflect a genetic trail of the postglacial migration route of E. coccifera.

In contrast to the classical ideas on population "bottle-necks" (Mayr 1963), it is suggested that in genera, such as Eucalyptus, where reproductive barriers are weak, "bottle-necks" may be associated with a dramatic release of variability arising from hybridization and this may have important evolutionary ramifications. Peripherally isolated and ecologically marginal populations play a central role in evolutionary theory (Mayr 1963; Endler 1977). The combined effects of isolation, population size (Mayr 1963), and atypical, or catastrophic (Lewis 1962), selective regimes make the probability of extinction high. Nevertheless, Levin (1970) noted that "major shifts in the adaptive mode and successful expansion from refugia are of sufficient frequency to render the species border an area of active speciation". Directional selection may result in a species being resurrected from its genetic remnants in a variable gene-pool (Kirkpatrick and Brown 1984). However, it is also possible that in a co-adapted multi-genic system, a different genetic starting point, along with chance events, may lead to a unique evolutionary product despite an identical selective environment. While Mayr (1963) stressed the potential for a "genetic revolution" associated with the loss of genetic variability

during population "bottle-necks", Levin (1970) argued this may also arise in peripherally isolated populations following hybridization disrupting developmental homeostasis and this may serve as a stimulus for major bursts of evolutionary change.

CONCLUSIONS

In conclusion, we emphasize the significance of both historical and ecological factors as determinants of the patterns of variation in the Tasmanian high altitude eucalypts. The extant variation patterns can at least partly be explained in terms of a response of populations to past fluctuating selective forces. Reticulate or anastomosing evolution is probably common, with both primary (parapatric and allopatric) differentiation and hybridization being important evolutionary processes. The classical ideas of population "bottle-necks", arising from founder events or range restriction, resulting in a reduction of variability should be re-assessed. In genera such as Eucalyptus, the genetic interaction with potentially interbreeding species could result in a dramatic release of variability in peripherally isolated populations which may have important evolutionary consequences.

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Eucalyptus pauciflora subsp. niphophila forms the treeline in the Kosciusko alpine area. The shape of the tree is a response to cold, strong winds and weight of winter snow. Photo C.J. Totterdell

FLORA and FAUNA of **ALPINE AUSTRALASIA**

Ages and Origins

Edited by
Bryan A. Barlow



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Cover: Etheridge Range, Kosciuszko
Alpine Area, in summer. *Ewartia*
nubigena and *Helipterum albicans*
subsp. *alpinum* in foreground.
(Photo: C. J. Totterdell)

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